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Most morphological and reproductive traits in maize, particularly those of economic importance, are classified as multigenic or quantitative. Even traits, such as disease resistance, frequently considered to be more simply inherited, might be 'semi-quantitative' in that trait expression is governed by several genes (often a major gene plus several modifiers).

Historically, one of the first questions in quantitative genetics asked whether the inheritance of these continuously distributed traits was Mendelian<sup>1</sup>. It is obvious that the answer to this question has had major implications in the mapping and manipulating of quantitative trait loci (QTLs). Several early investigations<sup>2,3</sup> supported the rejection of the 'blending' inheritance hypothesis and contributed to the conclusion that Mendelian principles apply to quantitative as well as to qualitative traits. During the 20th century, both plant and animal geneticists have obtained convincing evidence for the shaping of the general model that embraces the multiple-factor hypothesis for quantitative traits (with genes located in chromosomes and, hence, sometimes linked, and incomplete heritability because of the contribution of environmental factors to total phenotypic variation).

## Earlier investigations in maize

Several pioneering studies were conducted in maize during the 1970s and early 1980s that established the association of marker genotypes with quantitative trait performances<sup>4–6</sup>. These investigations provided much of the impetus for the recent flurry of activity in the use of genetic markers (isozymes and DNA-based markers) for identifying and mapping QTLs. In some of these earlier studies<sup>7,8</sup>, frequency changes of alleles at a large number of isozyme marker loci were monitored over different cycles of long-term selection in several populations of maize. Changes of allelic frequencies at several loci were shown to be highly correlated with changes in the selected trait, grain yield. Other studies<sup>9–11</sup> also showed associations between isozyme marker genotypes, and several morphological and reproductive traits in maize.

Results from the above studies led to a number of mapping investigations in several F<sub>2</sub> populations and in populations of recombinant inbred lines in maize. These studies<sup>12–15</sup> involved numerous plant characteristics, including dimensions, weights, and counts of vegetative and reproductive plant parts, as well as silking and pollen-shedding dates. In general, these earlier

# Mapping and manipulating quantitative traits in maize

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*Maize has been used effectively as a model organism in the development and evaluation of molecular markers for the identification, mapping and manipulation of major genes affecting the expression of quantitative traits in plants. Although quantitative geneticists have recognized the possibility of major loci, the general dogma had emerged that quantitative traits were controlled by many loci, each with a small effect. This interpretation sent a signal to the molecular biologist not to bother with quantitative traits because it would be essentially impossible to isolate a gene responsible for the trait. Recent results from numerous mapping studies have shown that quantitative traits are controlled by, at least some, factors with major effects, and have given credibility to the conclusion that major loci exist and that one might be able to study them. Positive results from marker-facilitated selection and introgression studies have further strengthened this conclusion.*

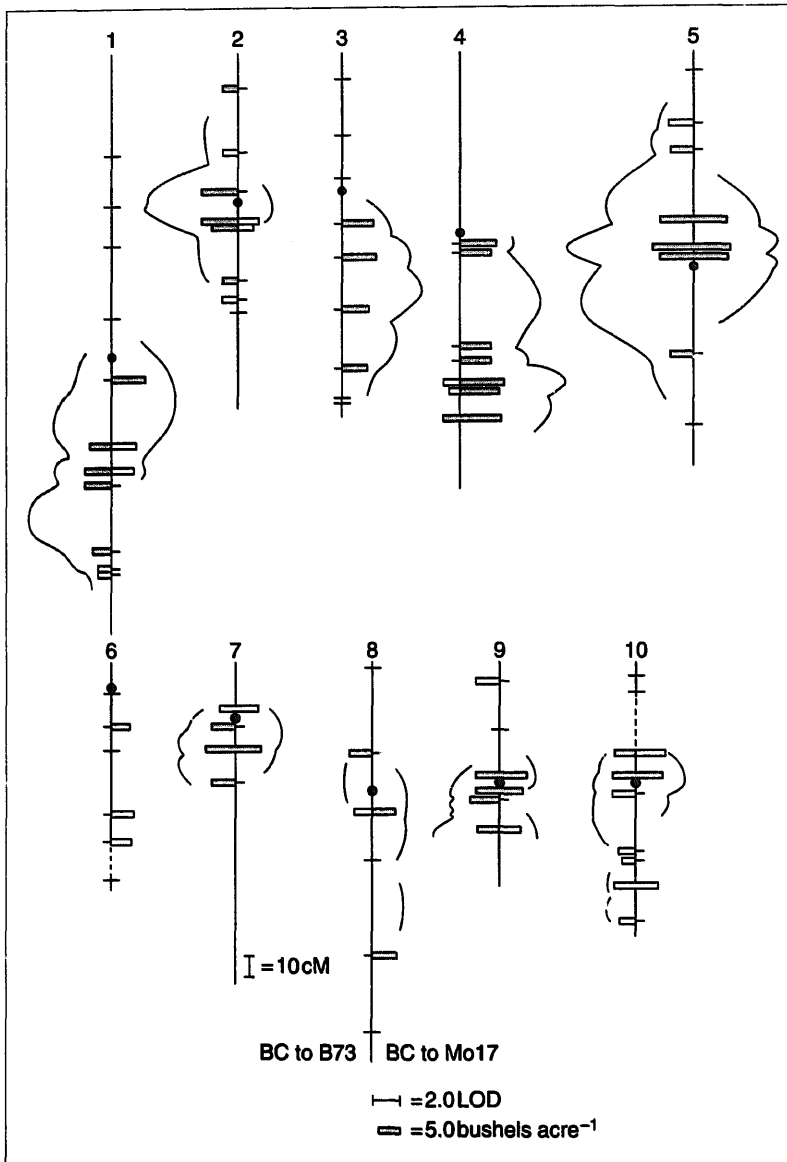
mapping investigations showed that QTLs affecting a number of quantitative traits were distributed throughout the genome. However, certain chromosomal regions appeared to contribute greater effects than others. It is also of interest to note that 'cryptic' factors were frequently uncovered in these and more recent investigations. For example, genetic factors contributing to high grain yield and tall stature occasionally have been associated with marker alleles from low-yielding, short-statured parental lines<sup>16</sup>.

## QTLs affecting grain yield

### Genomic mapping

The trait that receives the major emphasis in most maize breeding programs is the yield of grain. This trait, probably the most complexly inherited quantitative trait in maize, also has received the major focus in many mapping studies.

In the investigations of F<sub>2</sub> populations cited above<sup>12,13</sup>, only isozyme marker loci were employed for mapping genetic factors influencing the quantitative traits studied. A re-evaluation of one of the populations (CO159 × Tx303)F<sub>2</sub> was conducted both using restriction fragment length polymorphisms (RFLPs) and using



**FIGURE 1.** Maize chromosome map showing location of quantitative trait loci (QTLs) affecting grain yield in the backcrosses to the inbred lines B73 and Mo17 evaluated in six environments. The map summarizes the results of two analyses: interval mapping using LOD scores and single-marker three-factor analysis [accounting for set and location (environment) effects]. Interval mapping is represented by QTL likelihood plots showing LOD score curves exceeding the threshold of 2.0. Single-marker three-factor analysis is shown by bars protruding from the chromosome, whose length indicates the estimated phenotypic effect of substituting an allele at the QTL in the vicinity of the marker. Bars are shaded white or gray to show significant association exceeding the 0.01 and 0.001 levels, respectively. For all analyses, results from backcrosses to B73 are shown on the left and results from backcrosses to Mo17 are shown on the right of the vertical lines representing each chromosome.

isozyms as genetic markers<sup>16</sup>. By increasing the number of markers from 17 to 114, more accurate localization of QTLs was possible. Marker loci associated with several traits (including grain yield) generally corresponded well with the earlier results where comparisons were possible. However, a number of previously unmarked genomic regions were found to contain factors with large effects on some plant traits. Some of the genetic factors detected affected several yield 'compo-

nent' traits in a counterpoising fashion, thus producing no net effect on grain yield<sup>16</sup>.

In several of the more recent mapping studies in maize, parental lines were chosen to represent two different 'heterotic groups'. (Although it is difficult to define precisely a 'heterotic group', crosses made between lines within a group usually exhibit relatively less heterosis than crosses made between lines of different groups.) The two most widely used groups in US maize breeding programs are usually referred to as 'Iowa Stiff Stalk Synthetic' (BSSS) and 'Lancaster'. Most commercially grown single-cross hybrids are produced from crossing two inbred lines, one derived from each of these groups. Examples of inbred lines derived from BSSS are B73, B37 and A632; examples from the Lancaster group are Mo17, Oh43 and Va35.

The widely-used, highly productive inbred maize lines, B73 and Mo17, were used as parental lines in a major study to explore two important phenomena in maize genetics: heterosis and genotype-by-environment interaction<sup>17</sup>. With the use of 76 marker loci (9 isozyme and 67 RFLP, which were linked to about 95% of the genome), QTLs contributing to heterosis for grain yield were mapped on 9 of the 10 chromosomes in 264 backcross families (Fig. 1). For those QTLs associated with grain yield, the heterozygotes showed a higher phenotypic value than the respective homozygotes (with only one exception). The results, therefore, suggested not only overdominant gene action (probably pseudo-overdominance, i.e. nearby loci at which alleles having dominant, or partially dominant, advantageous effects are in repulsion-phase linkage), but also that the detected QTLs contributed significantly to the expression of heterosis in the B73 × Mo17 hybrid. Although the study was grown in six diverse

environments (four in North Carolina, one in Iowa and one in Illinois), there was little evidence for QTL by environment interaction<sup>17</sup>.

The data from the above study have been re-analyzed recently using a modification of the North Carolina experimental design III (Ref. 18). The latter analyses agree with the earlier report and strongly suggest the presence of multiple linked QTLs on most chromosomes that have significant effects on grain yield.

However, the results differ from the earlier report in that the design III analysis (a very powerful method for the evaluation of dominance variation) favors the hypothesis of dominance of favorable genes to explain the observed heterosis<sup>18</sup>.

Another mapping study<sup>19</sup> in materials derived from the inbred lines B73 and Mo17 was conducted and compared with the study<sup>17</sup> reported above. Although the two studies used materials derived from the same lines, the results showed striking differences in that many of the detected yield QTLs were not in the same regions. In the latter study<sup>19</sup>, it was speculated that the different results might be attributed to: (1) sources of the parental lines differed for the two studies; (2) type of progeny differed – backcrosses of  $F_3$  lines versus  $F_4$  progeny of  $F_2$ -derived lines; (3) different genotype-by-environment interaction effects; and (4) different small samples, 264 backcrosses versus 100  $F_4$  lines. The researchers concluded that the sampling of progeny is the most likely explanation for the differences. Both studies probably identified a valid subset of yield QTLs in B73  $\times$  Mo17; the lack of congruency suggests that the number of QTLs is likely to be large.

In another mapping study<sup>20</sup>, only one QTL for grain yield was reported in a cross of two lines, Mo17 and H99, which are both from the Lancaster heterotic group. However, 14 chromosomal regions were associated with yield-component traits. The objective of a somewhat different study<sup>21</sup> was to identify donor 'alleles' in a variable maize population for incorporation into Mo17, which would then be expected to improve the B73  $\times$  Mo17 single cross. In this study, the researchers found marker-grain yield QTL associations on nine of the 10 chromosomes.

#### Mapping variation

Although the documented number of maize populations evaluated for grain yield QTLs probably exceeds 40 (more than 20 have been studied in the author's research program), each population has shown a unique distribution of genetic factors significantly associated with the yield trait. Some chromosomal regions (such as 1L, 5S and 6L) show QTLs in a preponderance of the reported investigations. Other regions show significant associations with yield only rarely. It should be noted, however, that at least one grain yield QTL has been reported on each of the 20 chromosome arms of maize.

Magnitudes of the effects associated with specific QTLs varied greatly among reported investigations. In one study<sup>13</sup>, the number of plants measured in each of two  $F_2$  populations (1776 and 1930 plants) was adequate to detect factors contributing as little as 0.2% of the phenotypic variation in several yield-related traits. In another study<sup>17</sup>, nearly 20% of the phenotypic variation could be attributed to a region in the vicinity of the isozyme marker *Amp3* on chromosome arm 5S. When an analysis was performed in which much of the environmental variation was removed, that region accounted for nearly 35% of the estimated genetic variance for grain yield<sup>17</sup>.

Variation among investigations and among populations can logically be expected for the following reasons. (1) Detection of QTLs is dependent on polymorphism in the population studied. The number and

location of polymorphic regions affecting the trait differ among populations. (2) In some studies, specific genomic regions have lacked segregating markers. Thus, QTL detection would not be possible in those regions. (3) Environments for field evaluations differ and genotype-by-environment-interaction effects might affect the expression of certain QTLs. (4) Because of the small sample size used for many of the studies, sampling variation can affect the detection of QTLs<sup>19</sup>.

#### Fine mapping

Reducing the size of the regions identified as containing major QTLs through 'fine mapping' has been envisioned as an initial step in identifying single genes that ultimately could be manipulated using transformation (recombinant DNA) technology<sup>5</sup>. For example, as shown above in the population derived from the cross of B73 with Mo17<sup>17</sup>, a region in the vicinity of isozyme marker *Amp3* on chromosome 5 accounted for about 20% of the phenotypic variation for grain yield. This region has been targeted for fine mapping and it has been determined that there are at least three QTLs contributing to grain yield expression in this genomic region<sup>22,23</sup>.

#### Manipulating

A major goal for the use of genetic markers is to increase the efficiency of plant breeders by reducing the length of time for developing new lines and hybrids and, at the same time, increase breeding precision. Two of the earlier investigations in the use of markers for this purpose were conducted in open-pollinated maize populations and showed that selections based solely on manipulations of allelic frequencies at a small number of isozyme loci significantly increased grain yield<sup>24,25</sup>. Although the successes of these earlier investigations were not dramatic, they did provide the impetus for further use and development of marker technology as a tool for more efficiently breeding and manipulating quantitative traits.

In a more definitive study, selections were based solely on marker genotypes of plants that had been evaluated as  $F_2$  lines from crosses of two divergent maize inbred lines<sup>26</sup>. In one of the populations, a single cycle of selection for increased yield produced 20% more grain than the unselected  $F_2$  population. In that study, marker-facilitated selection (based on only 15 isozyme marker loci, which probably represented no more than 30–40% of the maize genome) was as effective as selection based only on phenotypic expression, which would be expected to affect the entire genome.

When the study cited above<sup>17</sup> in the population generated from the cross of the lines B73 and Mo17 was conducted, a companion study also was completed to identify and map QTLs in two highly productive, commercially used lines, Tx303 and Oh43. Earlier mapping studies<sup>12,15</sup> suggested that these lines contained genetic factors that might contribute to the heterotic response in the B73  $\times$  Mo17 hybrid. Six chromosomal segments were identified in Tx303 that (if transferred into B73) would be expected to enhance the B73  $\times$  Mo17 hybrid response for grain yield. Likewise, another six segments were identified in Oh43 for transfer into Mo17 to enhance the B73  $\times$  Mo17 hybrid<sup>27</sup>.

**TABLE 1. Grain yields of five high-yielding single-cross hybrids developed by crossing 'enhanced' B73 lines with 'enhanced' Mo17 lines**

		Grain yield (Bu acre <sup>-1</sup> )		
Maize line	Segment	1993	1994	Average
Enhanced lines				
B73 (248-6)	5S, 6L (Tx303)			
Mo17 (284-7)	3S, 10S (Oh43)	178.7	170.9	174.8
B73 (257-1)	6L (Tx303)			
Mo17 (271-8)	3S, 4S, 10S (Oh43)	178.1	169.5	173.8
B73 (198-2)	1S, 5S, 6L (Tx303)			
Mo17 (41-27)	4S, 9S (Oh43)	162.8	191.2	177.0
B73 (82-06)	3S, 5S (Tx303)			
Mo17 (271-9)	4S, 10S (Oh43)	160.8	189.3	175.1
B73 (198-2)	1S, 5S, 6L (Tx303)			
Mo17 (278-8)	3S, 4S, 10S (Oh43)	173.5	185.5	179.5
Controls				
B73 × Mo17		154.8	165.8	160.3
Pioneer hybrid 3165		156.4	169.7	163.1
SE <sub>d</sub> <sup>a</sup>		6.4	5.1	4.5

<sup>a</sup>Standard error of mean difference for comparing controls with hybrids.  
Abbreviation: Bu, bushels.

Marker-facilitated backcrossing was used for transferring one to four of the desired segments into the target lines, B73 and Mo17. Following two cycles of testing of the 'enhanced' B73 and 'enhanced' Mo17 lines in appropriate hybrid combinations, results (Table 1) from replicated field evaluations grown in two years showed that the grain yield of the better 'enhanced' hybrids exceeded the unimproved B73 × Mo17 hybrid and a high-yielding commercial check by at least 10% (14–19 bushels per acre)<sup>26</sup>. These studies demonstrated that marker-facilitated techniques can be successfully employed for introgression of desired alleles at multiple loci for manipulation of complexly inherited traits in maize, such as grain yield.

### Mapping QTLs affecting plant height

Many of the genetic factors affecting the expression of plant height in maize have been found to map to genomic regions including major qualitative loci that are known to influence plant stature<sup>16,29</sup>. In an F<sub>2</sub> population generated from the cross of inbred lines CO159 and Tx303, about a half of the 18 detected regions affecting plant height were also in the vicinity of previously mapped loci affecting plant stature<sup>16</sup>. In four populations of F<sub>4</sub> progeny derived from F<sub>2</sub> lines, a preponderance of the detected plant height QTLs were also found to be located in the vicinity of previously mapped qualitative loci known to influence plant stature<sup>29</sup>. In a study of two populations conducted in Italy, the number of plant height QTLs identified was less than noted above<sup>30</sup>. However, all QTLs identified were located in the proximity of major genes that affect plant stature and were in regions where QTLs for plant height were identified in the above two studies.

Seven QTLs were found to affect plant height in one population and four in the second population of European flint maize lines<sup>31</sup>. No attempt was made to correlate their results with qualitative trait loci in that study.

Another strategy for mapping quantitative trait genes, the 'candidate gene' approach, attempts to correlate variation in a quantitative trait with a candidate gene in a related biochemical or physiological process. Using this approach, the *Dwarf3* (*d3*) gene has been implicated as being responsible for quantitative trait variation in plant height associated with a region on maize chromosome 9 (Ref. 32).

### Mapping pest resistance traits

Although disease and insect resistance in maize is frequently considered to be simply inherited, several resistance traits have been found to be associated with multiple genetic factors. For example, seven genomic regions were found to be significantly associated with second-generation corn

borer resistance<sup>33</sup>. Damage from this pest is evaluated by measuring the length of tunnels in infested stalks. For the trait, tunnel length, the seven putative QTLs were responsible for 38% of the phenotypic variance.

The severity of the fungal disease, gray leaf spot, has increased in recent years. RFLP markers were used to map factors affecting resistance to this disease in three maize populations<sup>34</sup>. Although several putative QTLs were found in specific environment–population combinations, only one region on chromosome 2 was found to be consistently associated with resistance to gray leaf spot in all three populations when evaluated in several environments. In a mapping study of maize resistance genes for anthracnose stalk rot, only one significant QTL was found, on chromosome 4, in the two populations studied<sup>35</sup>.

### Mapping QTLs affecting other traits

Mapping factors affecting physiological traits has been the objective of several studies in maize. For example, six RFLP markers were found to be significantly associated with low-phosphorus stress<sup>36</sup>. In another study of a physiological trait, thermotolerance, six QTLs were detected that accounted for 53% of the genetic variability for this trait<sup>37</sup>.

Eight markers showed significant associations with CO<sub>2</sub> exchange rate in a study designed to evaluate RFLP marker stability. Moreover, RFLP markers were identified that were relatively insensitive to environmental effects and, thus, would be suitable for marker-assisted selection experiments<sup>38</sup>.

A study of QTLs affecting protein and starch concentration in the Illinois long-term-selection maize strains showed that 22 marker loci distributed on 10

chromosome arms were significantly associated with protein concentration<sup>39</sup>. Nineteen markers on nine chromosome arms were significantly associated with starch concentration. Sixteen of these were associated both with protein and with starch.

## Conclusions

The value of molecular-marker technology has been demonstrated to be effective for identifying and mapping QTLs in maize, as well as in several other crop plants. Also, the positive results from marker-facilitated selection and introgression studies should encourage the use of this technology for transferring desired genes between breeding lines<sup>5</sup>. Markers should increase the precision and efficiency of plant breeding, as well as expedite the acquisition of important genes from exotic populations or from wild species. However, at least one study in tomato shows that evaluations of identified factors in appropriate genetic backgrounds is essential before establishing breeding programs based on associations of markers with quantitative traits<sup>40</sup>.

Results from recent studies showing the high degree of homology and synteny between sorghum and maize genomes<sup>41–45</sup> should greatly enhance the efficiency for mapping quantitative traits in both species. In addition, comparative mapping with other monocotyledons has demonstrated many examples of conserved gene order and functions<sup>46</sup>, which should prove very useful in identifying and mapping useful genes in maize.

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